Encoding Induced Alpha EEG Activity Reveals Visual Working Memory Representations and their Manipulations

by

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Abstract

Until recently, the fields of visual working memory and imagery have independently studied the cognitive representation of visual information. It remains unclear, however, whether the representation of information during working memory and mental imagery are mediated by similar mechanisms, or whether they represent distinct processes. Previous studies have reconstructed orientation selectivity profiles from induced alpha-band (8 – 12 Hz) oscillations of electroencephalographic (EEG) data, enabling the identification of the contents held in visual memory. In an attempt to draw a bridge between these two fields, this thesis examines whether the induced alpha activity that has been shown to mediate the representation of orientations held in visual working memory can be used to track an imagery manipulation of these representation via a mental rotation. The results replicate previous findings, revealing that induced posterior alpha-band activity contains sufficient information that allows for the identification of the representation maintained in working memory. Furthermore, the reconstruction of orientation selectivity profiles revealed reliable changes in the mental representation during the imagery manipulation, although without being able to reliably decode the direction of the rotation. These results begin to bridge between isolated fields, indicating that these mental representations may depend on similar neural processes.

Keywords: Visual working memory, imagery, forward encoding model, mental representation, induced alpha activity

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BOLD	=	Blood-oxygen-level dependent
CC	=	Counter-clockwise
CDA	=	Contralateral delay activity
CTF	=	Channel tuning function
CW	=	Clockwise
EEG	=	Electroencephalogram / Electroencephalography
EOG	=	Electrooculogram / Electrooculography
ERP	=	Event-related potential
fMRI	=	Functional magnetic resonance imaging
IM	=	Imagery
ITI	=	Inter-trial interval
MVPA	=	Multi-variate pattern analysis
PET	=	Positron emission topography
rTMS	=	Repetitive transcranial magnetic stimulation
SPCN	=	Sustained posterior contralateral negativity
WM	=	Working memory

Encoding Induced Alpha EEG Activity Reveals Visual Working Memory Representations and their Manipulations

In the past few decades, we have observed a rapid development in new interdisciplinary fields of research that bridge between subject areas that do not necessarily appear to have anything in common at first glance (e.g. Neuro-marketing, computational political science, etc.). Despite these exciting new developments, some subfields of a shared discipline appear to be studying very closely related topics, without interacting for decades. For example, in 2013, Tong published a review article describing this phenomenon in cognitive science, in which he argued that the sizable fields of visual imagery and visual working memory are addressing the same underlying neural mechanism responsible for the representation and transformation of visual information (Tong, 2013).

According to their respective definitions, imagery and visual working memory are comparable processes as they are partially characterized by the capacity to manipulate mental representations of information (Tong, 2013). On the other hand, the major distinction between these two concepts relates to the origin of these representations; while visual working memory relies on perceptual information coming from the senses to create representations that are actively maintained (Baddeley & Hitch, 1974), imagery is better defined as a form of representation produced from memories that can be dynamically manipulated (Kosslyn, Ganis, & Thompson, 2001). The literature, however, is not very diligent on the use of these concepts. When the two concepts are being investigated at the same time, however, visual working memory is commonly limited to holding visual

information in active memory whereas performing any type of manipulation on the visual information is then referred as an imagery task (e.g. Albers, Kok, Toni, Dijkerman, & de Lange, 2013). Tong (2013) has expressed how these fields have failed to address the possibility that similar processes may be driving the very phenomenon that is at the core of their research, while providing evidence of recent studies that indeed point towards comparable neural mechanisms. There remain, however, a number of important gaps in the literature that relate the two processes. For example, although some studies have managed to relate specific neural activity with specific mental representations in visual working memory (Cichy, Ramirez, & Pantazis, 2015;Anderson, Serences, Vogel, & Awh, 2014; Foster, Sutterer, Serences, Vogel, & Awh, 2016), it is not clear whether the same activity also underlies mental imagery. Consequently, the aim of the present thesis is to identify brain activity associated with the decoding of visual working memory representations, and examine whether it is possible to decode transformed representations in mental imagery from the same activity.

Mental representation of visual information

The well renowned behaviourist B.F. Skinner once wrote that: "There is no evidence of the mental construction of images to be looked at or maps to be followed. The body responds to the world, at the point of contact; making copies would be a waste of time." (Skinner, 1977, p. 6) This approach towards mental representations, known as the propositional representation, suggests that we maintain visual information in a language-like format that only conveys the essence of visual information (Marr, 1982). It also implies that the subjective experience of

'seeing' an object via one's imagination is epiphenomenal – a by-product of neural processing that does not provide any functional purpose (Pylyshyn, 1973; Kosslyn & Thompson, 2003). Some evidence, however, is more consistent with a depictive/pictorial format rather than a propositional one (Pearson & Kosslyn, 2015). Indeed, Shepard & Metzler (1971) demonstrated that there is a direct positive correlation between the time required to perform a mental rotation of an object and the magnitude of the transformation supporting the idea that the object was recreated cognitively and rotated in the same fashion one would with a physical object. Similarly, the time necessary for participants to identify features of a drawing held in memory is directly related to the spatial distance between these elements (Kosslyn, 1973). These studies provide support to the idea that our mental representations of visual stimuli are not a set of descriptors, as the propositional format would indicate, but they are rather recreated in our mind in a depictive/pictorial form. It also suggests that the manipulation of mental representations follows a sequence that is similar to the perception of a physical object that undergoes a comparable transformation (Kosslyn, Ganis, & Thompson, 2001).

There is, however, support on the side of the propositional hypothesis as well. Since the beginning of the debate, Zenon Pylyshyn has been providing evidence for the representational format, as well as alternative reinterpretations of studies that originally supported the depictive/pictorial format (Pylyshyn, 1973). For instance, Pylyshyn revisited Shepard & Metzler's (1971) study and demonstrated that the type of imagery transformation, the stimulus attributes and

practice have greater effects on reaction time (Pylyshyn, 1979). It is therefore difficult to attribute the delay in reaction time during a mental rotation task to be a determinant criterion to discriminate between the depictive and propositional formats. On the other hand, some of the most compelling studies that advocate the propositional hypothesis come from studying visually impaired individuals. By measuring the time necessary to perform a mental rotation of tactile shapes by congenitally blind participants, Marmor and Saback (1976) were able to demonstrate that imagery does not depend on visual ability, as they were able to replicate Shepard and Metzler's (1971) findings. Interestingly enough, Marmor and Saback (1976) found no differences in the performance of mental imagery between congenitally blind, visually impaired and blindfolded normal individuals. Based on these findings, it remains unclear what the cognitive mechanisms are that support mental imagery.

In contrast with the imagery field of research, the working memory literature took a psychophysical approach and strived for direct measurements of memory ability rather than describing the nature of the representational medium. One of the earliest attempts at quantifying working memory capacity was from Miller's (1956) work, where he described a general working memory ability to retain seven bits of information on average across modality. In terms of visual working memory capacity specifically, however, Luck and Vogel (1997) demonstrated in a series of change detection experiments that individuals could easily retain up to four single-feature items (e.g., colored squares, oriented lines) before exhibiting a sharp decline

in change-detection accuracy when more than four items were displayed at the same time.

Studies of visual working memory capacity have given rise to a number of hypotheses that have attempted to describe the possible mechanisms behind visual working memory representations. Luck and Vogel (1997), for instance, proposed that this limited working memory capacity, which revolves around 3-4 items, may be explained by the presence of discrete compartments where each item to be remembered is stored. Due to the limited amount of 'slots' available to store a larger number of elements, items that fail to be maintained in one of these 'slots' will therefore not be available for recall. On the other hand, with the advancement of new experimental designs and data modeling techniques, recent work has been in favour of a flexible resource allocation approach to memory storage (Bays & Husain, 2008), which describes working memory as a process that distributes a limited amount of resources to every element to be remembered, rather than the all-or-none process described by the discrete 'slot' hypothesis. Using a continuous response recall task, Wilken and Ma (2004) demonstrated that working memory storage may not be limited to four items, but instead is affected by internal noise that increases proportionally to the number of items remembered, resulting in a decrease in the precision or fidelity of the stored representations. Working memory capacity was therefore described as a by-product of the interference in memory maintenance, not as a fundamental limit of working memory process. Just as the imagery field, the details of how the working memory representation are being held and processed are still heavily debated (Gorgoraptis, Catalao, Bays, & Husain, 2011;

Bays, Gorgoraptis, Wee, Marshall, & Husain, 2011; Zhang & Luck, 2008) and requires further investigation.

It does not seem clear, however, how these models of working memory representations can be integrated with the pictorial/propositional theories of imagery representation. Although the propositional and depictive debate has been raging for decades in the imagery literature, the visual working memory literature appears to often presuppose a depictive format without directly addressing the question. There seems to be some evidence that supports the idea that working memory engages a depictive format. Indeed, Thompson and Kosslyn (2011) demonstrated that a mask consisting of structured noise tends to create more interference in the recall task as this type of mask carries some information relevant to the task. These results suggest that working memory might partially rely on a depictive format. On the other hand, individual differences on mental imagery ability have been shown to play a major role in the strategy used during tasks that combine working memory maintenance and imagery manipulation. Indeed, Keogh and Pearson (2011) showed that individuals with greater capacity for imagery manipulation used a sensory-based imagery to complete the task and they tend to be disrupted by changes in background luminance, while those with poorer mental imagery abilities are not affected by the visual input and appear to rely on different strategies. They suggested that, while individuals better at imagery rely on a depictive format by engaging the sensory cortex, those with poor imagery abilities could employ higher level of processing that relies on a propositional format. Since research that compares working memory and imagery has only recently begun, it

remains unclear on whether these two processes use the same format to process visual information.

Cortical areas involved in perception and imagery.

Although behavioural measures alone have not been able to distinguish between the propositional and pictorial theories of mental imagery, numerous studies, notably from brain lesion studies, have suggested a strong overlap of the neural regions involved in mental representation and visual perception. In the 80s, a review of studies reporting visual impairments – such as achromatopsia, visual agnosia, etc. – resulting from lesions in the visual cortex described how comparable impairments are found in the production of visual imagery (Farah, 1984). Nonetheless, some exceptions have been reported where patients with cortical blindness were able to generate mental representations from memory (Chatterjee & Southwood, 1995) or that some patients with object agnosia are able to recall objects despite their inability to process objects perceptually (Jankowiak, Kinsbourne, Shalev, & Bachman, 1992; Behrmann, Winocur, & Moscovitch, 1992). These studies reveal that despite the fact that perception and imagery are intimately related processes, they are not completely indistinguishable in their neural organization.

With the development of neuroimaging techniques, it became easier to address the functional differences between visual and imagery processes. One study (Kosslyn, Thompson, & Alpert, 1997) compared the blood-oxygen level dependent (BOLD) contrast from functional magnetic resonance imaging (fMRI) between imagery and perception to determine the structures involved in each of these

processes. Two-thirds of the neural structures activated during normal perception, including primary visual cortex, were also recruited by imagery, which explains the exceptions depicted in brain lesion studies. Similarly, a causal relationship was established using repetitive transcranial magnetic stimulation (rTMS) coupled with positron emission topography (PET) on a mental rotation task (Kosslyn et al., 1999). Performance on an imagery task became impaired when the primary visual cortex was disrupted by TMS. These findings not only further describe how the processes involved in perception and mental representations are closely related but also depict how the primary visual cortex in particular is directly implicated in the manipulation of visual representations.

On the other hand, there is a growing body of evidence that suggests that the parietal and frontal lobes are recruited for the manipulation of mental representations as opposed to the primary visual cortex. fMRI studies have reported an increase in BOLD signals in the frontal and parietal cortical structures not only during the mental rotation of objects (Cohen et al., 1996; Kosslyn, DiGirolamo, Thompson, & Alpert, 1998; Richter et al., 2000; Jordan, Heinze, Lutz, Kanowski, & Jäncke, 2001; Ng et al., 2001) but also increases with working memory capacity during maintenance (Linden et al., 2003; Todd & Marois, 2004; Xu & Chun, 2006). It has also been suggested that a fronto-parietal loop might serve as an indication of a percepetual updating of the information held in working memory (Coull, Frith, Frackowiak, & Grasby, 1996). Moreover, training on a working memory task seems to increase the BOLD signals coming from a network of fronto-parietal areas (Olesen, Westerberg, & Klingberg, 2004), which reinforces the idea

that this cortical loop is involved in sustaining mental representations. Some studies have also provided evidence that the fronto-parietal network is also involved in the manipulation of the elements held in visual working memory. Indeed, a meta-analysis of fMRI studies, which has analyzed variations of the N-back task that manipulated the process and the content of visual working memory, has identified a robust activation of brain regions involved in in the fronto-parietal network (Owen, McMillan, Laird, & Bullmore, 2005). A causal relationship has also been established between the transfer of working memory to other cognitive tasks using transcranial magnetic stimulation (Kundu, Sutterer, Emrich, & Postle, 2013). These findings would support the idea that imagery may be a probable cognitive task that would engage the fronto-parietal network. The roles of the fronto-parietal loop and the visual cortex in mental representations and manipulation, however, are still a matter of debate and require more investigation.

Decoding mental representations.

The development of neuroimaging techniques has also brought a rise in methods for data analysis. Univariate analysis of neuroimaging data is traditionally performed to determine specific voxels – a three-dimensional pixel – that are significantly responding to the experimental manipulation by treating every voxel as a completely independent data point from the others (Davis et al., 2014). On the other hand, a decoding approach to neuroimaging data uses a multivariate voxel pattern analysis (MVPA), which allows for a more sensitive assessment of subtle changes in the activity pattern (Norman, Polyn, Detre, & Haxby, 2006). Decoding techniques have been widely used in fMRI studies for the past decade and have

allowed researchers to train pattern classifiers that can identify the stimulus associated with a particular pattern of brain activity (Davis et al., 2014). One of the greatest advantages of using MVPA is that the pattern classifier does not work from a set of a priori assumptions about the differences in mean BOLD signal between conditions and instead evaluates changes in the pattern of BOLD signal across a large number of voxels (Serences & Saproo, 2012).

Recently, fMRI studies have used MVPA to study working memory representations (Harrison & Tong, 2009) and their manipulations (Albers, Kok, Toni, Dijkerman, & de Lange, 2013). Harrison and Tong (2009) conducted an fMRI study where they looked at decoding simple grating patterns held in working memory from BOLD signals. They presented two grating patterns to participants, who had to hold both items in visual working memory until they were given a number cue to indicate which of the two stimuli was going to be probed at the end of the trial. The accuracy of the MVPA classification revealed not only were they able to initially decode (in the sense of predicting) both stimuli at above chance levels, but also that the classification accuracy for only the cued stimulus persisted following the cue, consistent with the presence of the visual stimulus held in working memory. It is important to note that the pattern classifier was trained on the BOLD signals generated in area V1 through V4, which demonstrates that there is sufficient information present in the visual cortex to identify mental representations no longer present in the display. These results have also been corroborated by other studies (Ester, Serences, Awh, 2009; Riggall & Postle, 2012), and it has been demonstrated that the activity decoded from visual cortex correlates with the

precision of representations (Emrich, Riggall, LaRocque & Postle, 2013), suggesting that these neural representations play a role in behaviour. Thus, the results from these fMRI studies that employ a decoding approach support the idea that the mental representation of a working memory stimulus can be found within the visual cortex.

Based on Harrison and Tong's (2009) working memory paradigm, Albers et al. (2013) introduced an imagery condition where participants were required to mentally rotate the cued working memory stimulus. The imagery condition used the same sequence as working memory paradigm described in Harrison and Tong's (2009) with the exception that a cue window was presented at the beginning of the trial providing the participant with a direction (clockwise or counterclockwise). Participants were then required to perform a 120° mental rotation of the cued item in the direction given at the beginning of the trial. In this fMRI study, the pattern classifier was trained on three grating patterns, which were used to decode the stimulus held in working memory as well as to track its manipulation through the mental imagery. During the working memory portion of the task, the classifier revealed greater evidence for the cued stimulus over the uncued stimulus, thus successfully replicating Harrison & Tong (2009). In the imagery condition, the authors were able to track and identify the transformed stimulus that corresponded to the mentally rotated pattern. That is, evidence for the original (memory) stimulus decreased, while evidence for the originally uncued (transformed) stimulus increased. Consequently, this study demonstrates that information about the transformed stimulus is present in the same regions as visual working memory

representations, and that it is possible to track the manipulation of mental representations using a decoding approach. Moreover, Albers et al.'s (2013) findings substantiate the overlap of working memory and imagery representation with perception, as demonstrated by their ability to decode these processes within the sensory cortex.

It is only in the past few years that MVPA has been attempted on EEG (Garcia, Srinivasan, & Serences, 2013; Anderson, Serences, Vogel, & Awh, 2014) and MEG (Cichy, Ramirez, & Pantazis, 2015) research, and has demonstrated some promising results. A fairly recent article has demonstrated that it is also possible to identify the working memory representation from EEG data. Anderson et al. (2014) employed a method proposed by Garcia et al. (2013) where the MVPA decoding technique was adapted to EEG recordings. In addition to the decoding approach, Anderson et al. (2014) used a forward encoding method, which recreates the pattern of neural activity associated with the stimulus based on a priori assumptions about how the neural activity relates to the stimulus (Serences & Saproo, 2012). While MVPA detects the changes across voxels or channels that are most reliable to identify differences between the type of stimulus (or conditions) presented, an encoding model uses the opposite approach by working from the stimuli themselves and making assumptions about the type of activity that is expected to be associated with the specific stimulus. In the context of studying the perception, memory, and manipulation of simple visual features, encoding models typically assume the properties of the neurons found in early the visual cortex (Serences & Saproo, 2012).

Using the two approaches of decoding and forward-encoding, Anderson et al. (2014) demonstrated that EEG activity can reflect features of the stimulus held in memory. Specifically, they were able to identify the frequency range in which the pattern classifier was the most effective at identifying the pattern associated with the mental representations. The induced time-frequency power estimates, which reflects non-phase-locked activity, showed increased activity between 4-20 Hz range during the task using both approaches, but the encoding model was only able to identify the orientation of a remembered stimulus in the alpha band (8-12 Hz). These results indicate that not only it is possible to keep track of mental representations by decoding EEG data but also that induced activity in the alpha band seems to carry information about the maintenance of working memory representations.

Due to a mistake in their data analysis, Anderson et al. retracted their article ("Author-Initiated Retraction," 2015). Despite the retraction of the article, Foster, Sutterer, Serences, Vogel & Awh (2016) used the same method in a recent paper and were able to uphold some of the findings observed in Anderson et al.'s (2014) study. Indeed, Foster, Sutterer, Serences, Vogel, & Awh (2016) were able to associate induced alpha activity with holding the spatial location of a stimulus around a circle using the same approach as in Anderson et al. (2014). These findings further support that induced alpha activity contains information about the specific features of visual stimuli held in visual working memory representations. Importantly, in both the Anderson et al. (2014) and Foster et al. (2016) studies, the induced alpha activity was recorded from posterior channels, consistent with the idea that the

maintenance of mental representations occurs within the visual cortex. Thus, in both fMRI and EEG, it is possible to decode mental representations from visual cortex. However, although it has been shown that it is possible to decode the transformation of mental images from fMRI (Albers et al., 2009), it is not clear whether the oscillatory activity associated with working memory representations (i.e., induced alpha activity) can also be used to track the transformation of mental images.

Current Study

The aim of the current thesis is to examine whether it is possible, using a forward-encoding model on EEG data, to track the manipulation of the contents of visual memory and imagery. More specifically, this experiment uses alpha time-frequency power of EEG signals to track the manipulation in working memory via an encoding approach. The objectives of the current thesis are twofold: first, to replicate the findings of Anderson et al. (2014) and Foster et al. (2016) by decoding information about a stimulus held in working memory from alpha-band EEG using a forward-encoding model. Second, to determine whether it is possible to track changes in these representations as they are being subjected to mental rotation, as Albers et al. (2013) have done using fMRI. Accomplishing these objectives will not only confirm previous findings that induced alpha activity appears to play a role in the maintenance of visual representations, but also comment on the nature of the mental representations during mental imagery.

Method

Participants

Participants consist of 10 Brock University students (3 males, 7 females) who were recruited from posters and from the Psychology Department Research Pool (SONA). A short interview was conducted to determine the eligibility for their participation (see Appendix A). Participants were screened for healthy individuals ranging between 17-30 years of age, with normal or corrected-to-normal (glasses or contacts) vision, with no history of serious psychiatric or mental health issues, no head injury, concussion, or loss of consciousness, and did not have any condition that may affect their nervous system. Qualifying volunteers were offered a compensation of $15/hour or 1 experimental course credit/hour for their participation.

Apparatus

The experiment was displayed on a 20-in LCD monitor with a resolution of 1600x1200 and a refresh rate of 60Hz. Participants were positioned approximately 60 cm away from the display and the responses were completed with a standard keyboard and mouse.

Stimulus and Paradigm

Stimulus. As demonstrated in the meta-analysis done by Thompson & Kosslyn (2000), using a high-resolution image that involves orientation is most likely to activate the primary visual cortex. Accordingly, a solid bar was used as the memory stimulus. This stimulus also replicates that of a previous study using the same type of stimulus (Anderson et al., 2014). Each trial presented a single stimulus

consisting of a line that spans the diameter of a circle (figure 1). This stimulus carries an orientation feature taken from one of 8 possible orientations bins divided equally between 0° and 180° (orientation bins: 11.5°, 33.75°, 56.25°, 78.25°, 101.25°, 123.75, 146.25°, and 168.75°). Each bin was centered around these 8 orientations with a window of ±11.5° to cover the 180° of possible orientations of a line.

Paradigm. The task consisted of 15 blocks of 64 trials (total of 960 trials) where each block randomly presented 8 stimuli from each of the 8 different orientation bins. In a single trial (see Figure 1), participants were instructed to stare at a black fixation point for 1000ms (with a 500ms jitter) during the inter-trial interval (ITI) window until a solid bar that spanned the diameter of a circle was presented for 250ms, conveying the specific orientation to be remembered. The sample stimulus was followed by a 500ms fixation display in which participants have to hold the orientation of line in visual working memory. After 500ms, the fixation point changed colour to cue the participant to perform a mental rotation on the memory stimulus during a 1500ms window. The direction of the mental rotation was determined by the colour of the cue, where a red fixation indicated a 60° clockwise rotation whereas a blue fixation indicated a 60° counter-clockwise rotation. Finally, participants were probed to report the orientation of the transformed stimuli by clicking at the location where either end of the diametrical bar would have crossed the circle, thus replicating Anderson et al.'s (2014) paradigm. Each block was separated by a short self-paced break.

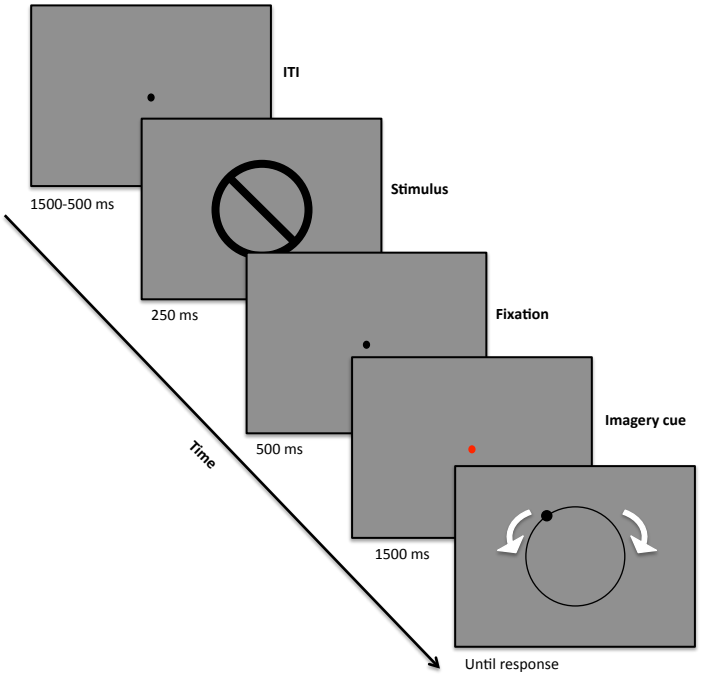

Figure 1. A schematic of a single trial of the behavioural paradigm. Trials begin with a fixation point presented for 1,000 ± 500ms. The sample stimulus was then presented for 250ms, followed by a fixation point for the delay window of 500ms. After the initial working memory delay period, participants were cued, via a change in the colour of the fixation, on the direction of the mental manipulation to be performed. The rotation cue was present for 1,500ms. Finally, a probe window appears that required the participants to report the orientation of the transformed stimulus using a mouse click.

Procedure

Participants were greeted and asked to read, complete and sign the consent form (see Appendix B). After completing a demographic questionnaire and reviewing the screening criteria for the study, participants were instructed on the steps of EEG setup before it was carried out. The steps include scalp measurements, cap fitting, inserting the electro-conducting gel in the cap, and placing scalp and face electrodes. Participants were then instructed on the task and ran through a series of practice trials (~ 2 blocks of 32 trials) before beginning the actual experiment. In addition to the small breaks between the each block, participants were offered a

longer break halfway through the experiment where a light snack and drink was provided. This entire procedure generally took ~2hrs to complete.

Behavioural Data

Because this paradigm uses a diametrical line as the stimulus to convey the orientation feature of the stimulus, participants could only report an angular difference spanning over -90° to 90°. Mean error of the response was calculated as the difference between the target (rotated) orientation and the participant's response. Using the MemFit.m function of the MemToolbox MATLAB extension (Suchow, Brady, Fougnie, & Alvarez, 2013), maximum likelihood estimates of a two-component mixture model (Zhang and Luck, 2008) were calculated. This method separates responses into guesses, estimated from the height of a uniform distribution – since guess responses are assumed to follow a uniform distribution (increasing in height as guess responses rise) – and the precision of correct responses given by the spread of the von Mises (circular normal) distribution (i.e. standard deviation) – where precision increases as the distribution narrows (see Zhang & Luck, 2008). In addition, trials that were more than 30° error (in either direction) away from the target response were rejected from the analysis. (Mean behavioural rejection = 3.31%)

EEG Data Acquisition

All recordings were performed using a BioSEMI system through Ag-AgCl electrodes with built-in amplifier at a sampling rate of 512 Hz. Sixty-four electrodes with on-line reference to the CMS/DRL were positioned according to the extended 10-20 configurations, along with 6 additional skin electrodes: 2 mastoids for

reference, 2 vertical and 2 horizontal extraoculogram (VEOG and HEOG) channels placed ~1 cm below and beside the eyes. Only 16 electrodes corresponding to the posterior sites of the international 10-20 system of 64 electrodes apparatus were used for the encoding analysis (channel locations: PZ, P1, P2, P3, P4, P5, P6, PO3, PO4, PO7, PO8, POZ, OZ, O1, O2, and IZ). All channels were re-referenced off-line to the average of the left- and right-mastoids. Horizontal eye movements were detected by identifying square waves in the VEOG channel that exceeded 32μV, which reflects lateral eye movement, and eye blinks were identified using peak-to-peak difference in the HEOG channel that exceeded 80μV. Trials contaminated with blinks or lateral movements were rejected (mean artifact rejection = 22.79%).

Data Analysis

The forward encoding model used in this analysis is based on the principle that the activity detected by each electrode is not only caused by a large number of neurons that are sensitive to the particular feature of interest (i.e., orientation), but also more responsive to particular features over others. This pattern of response is assumed to follow the neural population coding distribution similar to tuning function of a single neuron, where each electrode should detect a decrease in the amount of 'preferred' activity as the stimulus presented moves away from the 'preferred' orientation. These idealized curves serve as a basis set for the tuning functions or 'channels'. Thus, for every electrode, a series of hypothetical tuning channels are created that correspond to the 8 different possible orientations, and these channels should theoretically respond to the variation in the stimuli according to their relationship to the 'preferred' channels. Accordingly, each electrode will

have a particular activity profile in response to the 8 different types of orientations presented. We can therefore describe the neurons generating the specific electrical activity as a weighted sum of the 8 tuning channels. To calculate the activity profile associated with these tuning functions, a subset of the total number of trials is used as a training set. Once these channel weights are estimated from this training data, a fit can be estimated by regressing the weights onto 'new' data from the test set, which correspond to remaining trials after the training set is removed, revealing the correspondence between activation in each channel, tuned to a particular orientation, and the stimulus present on a given trial.

All signal processing was conducted using MATLAB (www.mathworks.com) along with the EEGLAB Toolbox (http://sccn.ucsd.edu) and the Signal Processing Toolbox. MATLAB scripts from Foster et al. (2016), rendered public by the authors (https://osf.io/bwzfj/), were used and modified to generate the encoding model for this experiment.

Following from Anderson et al. (2014) and Foster et al. (2016), power values were estimated by first bandpass filtering the raw EEG data across a restricted frequency range with the help of the "eegfilt.m" function (Delorme & Makeig, 2004). Then, a Hilbert transform was applied to the filtered data to extract the complex analytical signal. This signal-processing step was performed within the alpha band ranging from 8-12 Hz. Evoked power, which reflects phase-locked components, and induced power, which reflects non-phase-locked activity, were derived using the following formulae:

$$Evoked\ Power = \ abs\left(\frac{\sum_{i=1}^{n}\left(hilbert\left(eegfilt(data_i, Sr, f_1, f_2)\right)'\right)}{n}\right)^2$$

$$Induced\ Power = \frac{\sum_{i=1}^{n}\left(abs\left(hilbert\left(eegfilt(data_i, Sr, f_1, f_2)\right)'\right)^2\right)}{n}$$

where $data$ is a matrix (electrode x time) of raw EEG signals for each trial i, n is the number of trials per block that for a given orientation and electrode, Sr is the sampling rate (512 Hz), f_1 is the lower bound bandpass frequency (8 hz) , and f_2 is the upper bound bandpass frequency (12 Hz).

To reconstruct the orientation-selective channel tuning function, the encoding model assumes that the EEG power recorded at each electrode is a weighted sum of the eight possible orientation channels where certain electrodes are better tuned for a specific orientation than others – following a neural population coding distribution. The basis set for the hypothetical tuning channel response profile can be described by a half-sinusoid function:

$$R = \sin\left(\frac{\theta}{2}\right)^7$$

where R is the hypothetical channel response and θ represents the angular orientation spanning between 0-180°. The equation is raised to the 7th power to create a narrower function that will allow adequate space for the 8 different tuning curves associated with every variation of the orientation feature. At each electrode site and for each tuning channel, the basis set was circularly shifted so that the peak of each tuning function corresponds to one of the orientation bins.

During the training phase of the analysis, weights (W: m electrodes $*$ k channels) can be estimated from a dataset (B_1: m electrodes $*$ n observations) of the

EEG power activity from each electrode site at each time point, and from the hypothetical channel response (C_1: k channels $*$ n observations), as depicted by the following relationship:

$$B_1 = WC_1$$

Therefore, we can estimate weight matrix through a regression analysis done via a least-square estimation (i.e. matrix division):

$$\widehat{W} = B_1 C_1^T (C_1 C_1^T)^{-1}$$

The obtained weights are then used in the testing phase with a new dataset (B_2) to estimate the channel responses (C_2) through regression:

$$\hat{C}_2 = \left(\widehat{W}^T \widehat{W}\right)^{-1} \widehat{W}^T B_2$$

Theoretically, if there is enough information in the training dataset activity that relates to the orientation of the cognitive representation of the stimulus, the weights calculated will be reliable enough to be applied to the testing set and recreate the basis set (or tuning function) for each hypothetical tuning channel, relative to each orientation. It is important to note that the training data set was constructed from a random selection of two-thirds of the total number of trials while the last third was used as the test set. This procedure was repeated for 10 iterations and the results were then averaged across iterations. Also, to minimize the effect of individual differences, the encoding procedure was completed separately for each participant.

Since the basis set used as the theoretical channel response of the training phase was circularly shifted before the encoding process, the resulting channel responses are then re-centered, which allows plotting the tuning channel offset relative to a common orientation.

Statistical Analysis

To perform the necessary statistical test on the results from the encoding model as described in Foster et al.'s (2016), the resulting channel tuning functions were linearly transformed by collapsing the corresponding points of the basis set that share the same distance from the center (e.g., +/- 15 degrees). The slope of this transformed curve was calculated by applying a linear fit, using the "polyfit.m" MATLAB function, which uses a line of best fit approach, and the slope of all tuning channels of each electrode were calculated at every time point. In order to test whether the results from the encoding model were statistically greater than chance, and since the channel tuning functions are not necessarily normally distributed, a null distribution was approximated by running the encoding procedure 1,000 times with randomized labels. This surrogate distribution was therefore used to calculate the t-statistic associated with the comparison of the actual data and the surrogate null at every time point. Additional statistics performed on behaviour and on mean slopes were performed using the "ttest2.m" MATLAB function.

Results

Behavioural results

In order to assess the performance of the individuals on the task, the participants' responses were modeled using Zhang and Luck's (2008) Mixture Model. By assuming that the pattern of all of the responses coming from a continuous report probe consists of a mixture of the stimulus held in memory (P_m) and a guessing factor (P_g), it is possible to extract the contribution of these two factors. In other words, the total response pattern comprises a combination of

correct reports and guesses ($responses = P_m + P_g$). Furthermore, by calculating the circular standard deviation in the correct responses, it is possible to assess precision (1/SD of the von Mises distribution). The guess and target rates as well as precision were estimated for all participants after behavioural and artifact rejection.

The overall performance across conditions reveals a low guess rate of 6.74%, a target rate of 93.3% and precision of 11.09°. In the clockwise imagery transformation condition, participants guessed their answers 8.6% of the time and successfully reported the target at 91.4% with a precision of 10.99° while, in the counter-clockwise transformation, they produced a guess rate of 4.94% and a target rate of 95.1% with a precision of 11.13°. These reasonably low guess rates and high target rates confirm that the participants accurately held in memory the orientation and reported the transformed stimulus with a high level of precision. To determine whether there was a statistically significant difference between clockwise and counterclockwise rotation for the imagery manipulation, two sample t-tests were conducted for both precision and guess rate. As expected, the pattern of responses is not significantly different in terms of SD, $t(18) = -.6204, p = .536, d = .297$, and with regard to P_g, $t(18) = .5925, p = .561, d = .279$.

Encoding Model Results

Working memory. The first objective of this thesis was to replicate Anderson et al.'s (2014) and Foster et al.'s (2016) findings, in which they were able to identify reliable information associated with working memory representations within the induced posterior alpha-band activity using a forward-encoding model. To assess the working memory (WM) part of this experiment, every trial belonging

to a particular orientation bin was grouped together regardless of the direction of the imagery manipulation. By ignoring the imagery (IM) manipulation part of the experiment, the neural activity generated within the first 750ms after the onset of the stimulus (0ms) of each trial allows for a direct replication of Anderson et al.'s (2016) line orientation paradigm. It is in the interest of replication that all the analyses were performed on the alpha band activity solely, which was selected by applying a bandpass filter between 8-12Hz.

As described in the methods section, the hypothetical channel response (a.k.a. basis set) is designed to have its highest peak centered at the orientation that corresponds to the presented stimulus. Therefore, the encoding model reconstructed the activity associated with eight orientation channels that are expected to peak at each stimulus' corresponding orientation. To visualize the reconstructed channel responses produced by the encoding model during working memory maintenance, the channel responses were aligned (i.e., centered to 0° independent of orientation bin), creating a set of eight channel offsets (i.e., +/- relative to the target orientation centered at 0°), and plotted over time. Thus, the resulting channel tuning functions (CTFs) can easily depict whether the presented orientation, regardless of which variation, was accurately represented by the encoding model by exhibiting a large peak channel response in the center of the CTF (i.e. 0° offset), representing a highly selective CTF, or not represented at all by presenting a relatively flat (or inconsistent channel offset).

The CTF of the evoked activity shows a slight increase in selectivity shortly after the presentation of the stimulus around 160-320ms (Figure 2A), suggesting

the evoked alpha activity accurately reflected the remembered orientation during this window. Taking an average of the tuning functions in this window (Figure 2C: black line), it becomes clearer that, despite depicting a very wide distribution of selectivity, the CTFs derived from the evoked activity peak around 0°, corresponding to the presented stimulus orientation. On the other hand, the induced CTFs depict a more sustained activity in the channel selectivity between 40-600ms and more particularly between 200-350ms) (Figure 2B). An average of the CTFs from the onset of the stimulus up to the end of the delay period shows quite clearly the selectivity peaking around the presented stimulus (Figure 2D: black line).

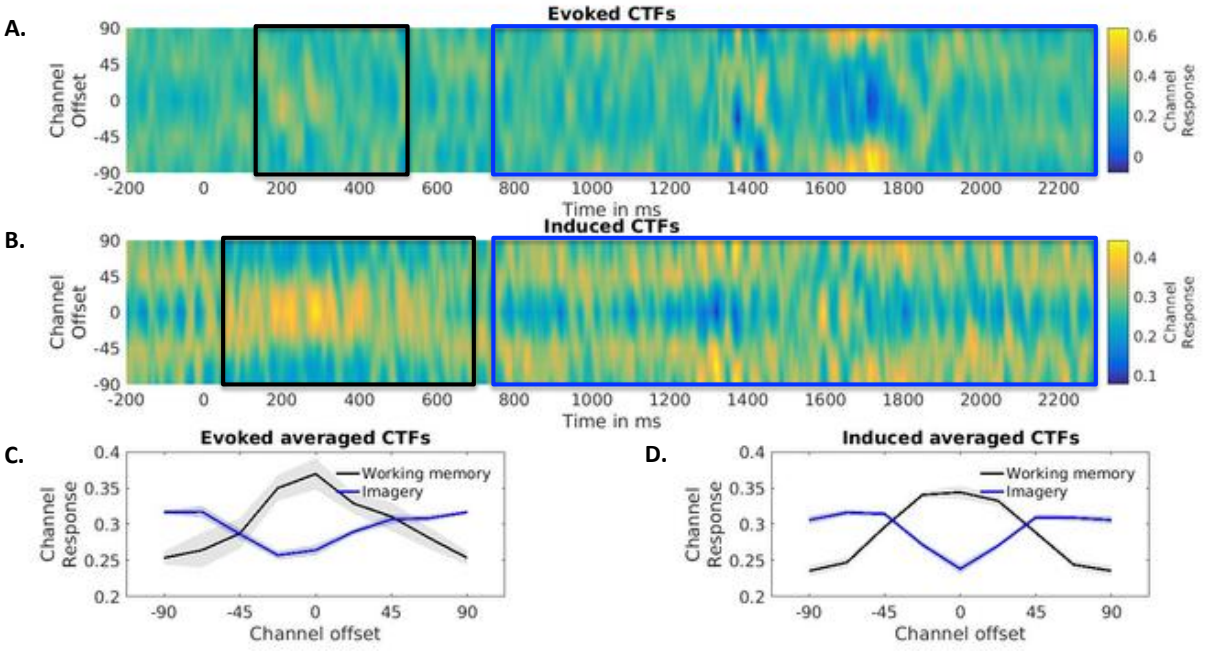

Figure 2. Orientation selectivity of alpha band (8-12 Hz) activity, independent of the mental rotation direction. The delay period begins at 250ms and the imagery cue at 750ms. **A**: Channel selectivity (relative to the sample orienation) of evoked power across time. 0 ms represents the onset of the memory stimulus. **B**: Channel selectivity of induced power across time point. **C**: Evoked CTFs profile averaged over the working memory phase (160-320ms) shown in black and the imagery phase (750-2300ms), depicted in blue. Channel offset is plotted on the x-axis, relative to the memory sample **D**: Induced CTFs profile averaged over a the working memory window (40-700ms) shown in black and the imagery

phase (750-2300ms), shown in blue. Shaded regions corresponds to a 99% confidence standard.

To discern whether these tuning function profiles are reliably above chance, the slopes (measured from +/- 90° to 0°) of the reconstructed CTFs were plotted across time (Figure 3). Additionally, in order to determine if the slopes of these reconstructed CTFs were significant, t-test comparisons with a surrogate null hypothesis were performed at every time point (as described in the Method section). Examining the evoked activity, the slopes of the tuning functions during the WM window are significantly above chance (Figure 3A), although this effect appears to be transient and unreliable. In contrast, the slopes of the CTFs calculated from the induced power are more consistent, reaching significance between almost the entire window from 200-600ms (Figure 3B). These results confirm Anderson et al. (2014) and Foster et al. (2016) that posterior induced alpha activity appears to contain stimulus-specific information about representations held in working memory.

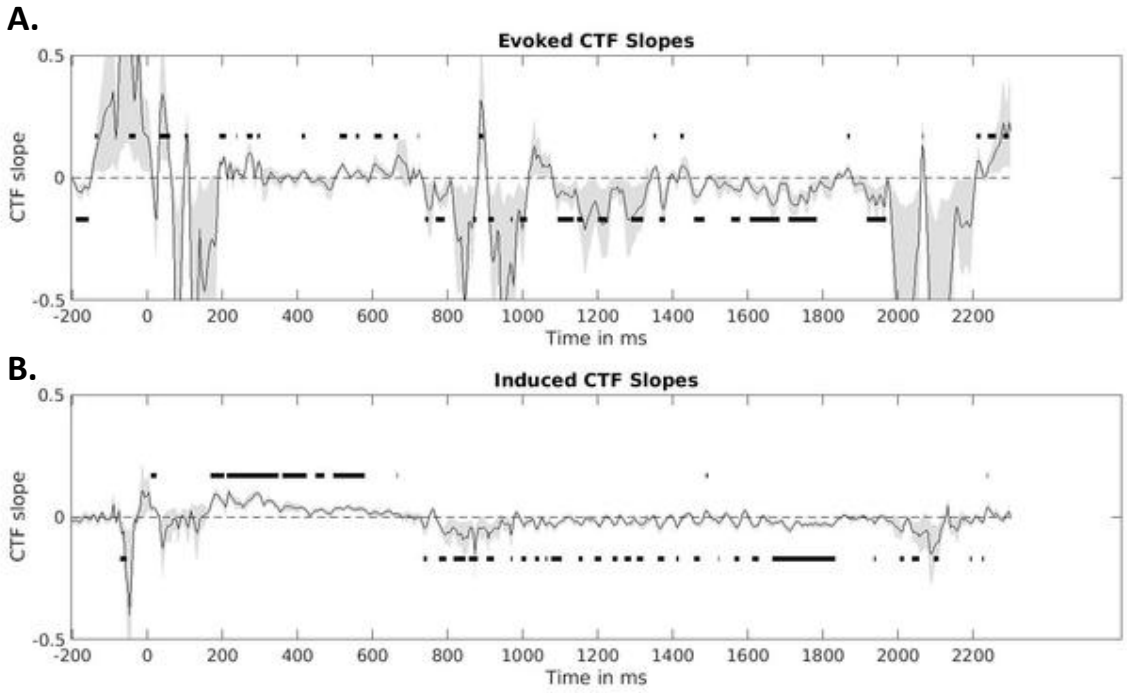

Figure 3. Slopes of the CTFs profile at every timepoint. Area of significant difference of a two-tailed t-test comparison with a surrogate null hypothesis at $p < 0.01$ are indicated by a solid black line over the baseline for a significant selectivity of the sample orientation CTFs, and below the baseline for significant selectivity away from the sample orientation. Shaded regions correspond to a 99% confidence. **A**: Evoked CTFs slope of alpha band activity. **B**: Induced CTFs slope of alpha band activity.

Although the activity during the imagery window was not the focus of this particular analysis, it is interesting to note that there is a decrease in the peak selectivity for the tuning channels that are sensitive for the orientation of the sampled stimulus and an increase peak selectivity in the channels whose offset is away from the sample stimulus, notably between 750-1500ms (Figure 2A-B). Again, this effect is even clearer when an average of the tuning channels is calculated, revealing peak selectivity for the channels away from the presented stimulus (Figure 2C-D: blue line).

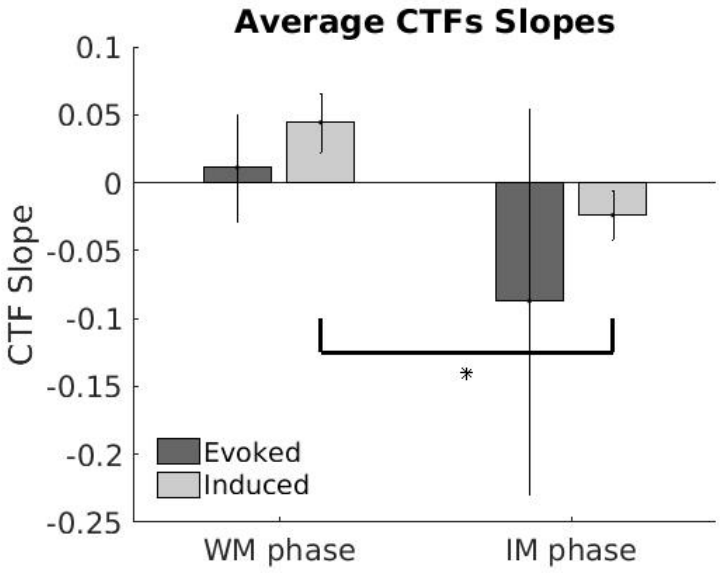

Figure 4. Average CTF slopes for evoked and induced activity across working memory and imagery phases, independent of mental rotation direction. Statistical comparison of induced activity between working memory and imagery window showed a significance at P < .005 (*).

To better compare the differences between the working memory and the imagery phases of the task, average CTFs slopes for both evoked and induced activity were calculated over two windows: the working memory phase (200-600ms) and the imagery phase (800-1800ms) (Figure 4). Two sample t-tests were conducted to determine whether these windows were statistically different. The slopes of the CTFs derived from induced activity were reliably different between the WM ($M = .0443, SE = .0216$) and IM ($M = -.0239, SE = .0179$) windows, ($t(18) = 4.52, p = 2.55e^{-4}, d = 2.13$). For the evoked activity, the slopes of the CTFs between the WM ($M = .0112, SE = .1418$) and the IM ($M = -.0872, SE = .1418$) windows were not significantly different, $p = .2298$. Thus, these results suggest that not only does induced activity encode the orientation of the

remembered stimulus, but that the encoded orientation of this stimulus significantly changes following the imagery manipulation.

Imagery. The second objective was to keep track of the transformation of the line orientation during the mental imagery (IM) phase, as it was hypothesized that these changes would be represented in the CTFs created from the induced alpha activity. Based on the WM analysis, there is already some evidence that the channel selectivity associated with the presented stimulus is decreased during the imagery period (Figures 2 - 3). To determine if it is feasible to keep track of the direction of the transformation, the encoding model was calculated separately for the two different imagery conditions (clockwise and counter-clockwise transformation), and then the counter-clockwise (CC) CTFs were inverted so that both transformations reflected a change in a clockwise (CW) direction. By averaging the CTFs of these two conditions, it becomes possible to determine whether the encoding model can only depict the absence of the presented orientation feature or if it can also denote the direction of the transformation applied to the mental representation by depicting a CTF shift in a single direction.

The resulting CTFs during the WM phase of the paradigm in both evoked and induced activity appear to be very similar to the results from the previous analysis (Figure 5A-B). The average of the CTFs of the evoked activity over 160-310ms and between 60-200ms for the induced activity produces greater selectivity for the orientation that matches the sample working memory stimulus, consistent with the analysis above. At first glance, the CTFs created from the induced activity during the WM phase appear to be shifted towards a more negative offset suggesting the

encoding of a representation that is more counter-clockwise than the sample stimulus orientation.

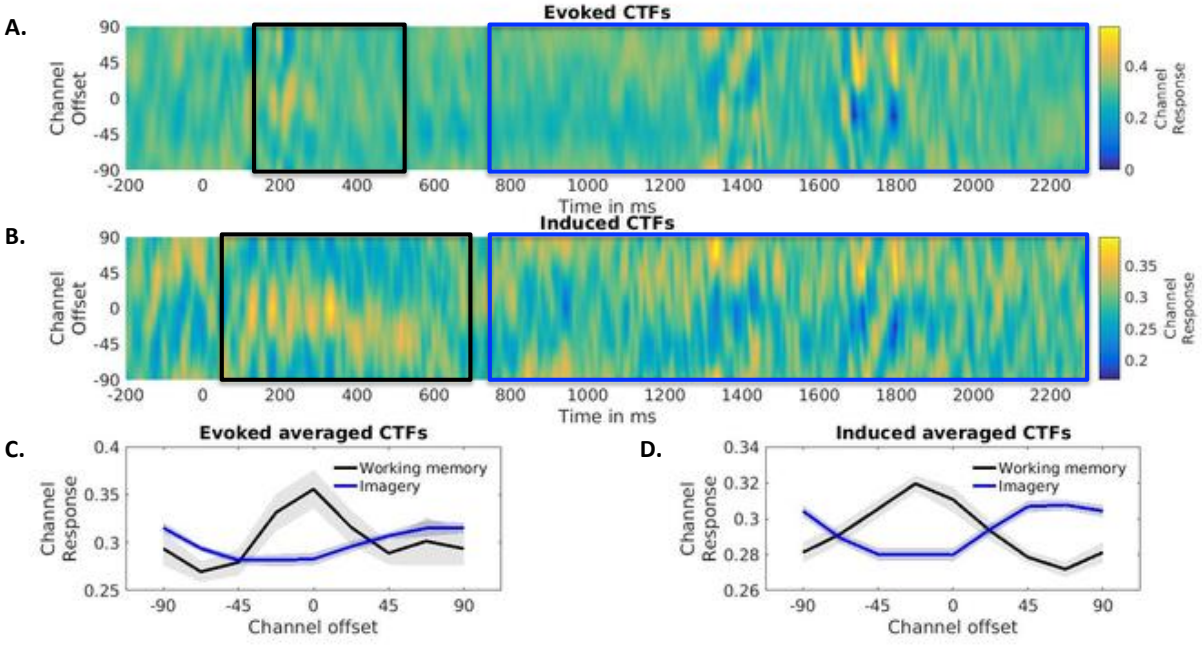

Figure 5. Orientation selectivity of alpha band activity for the imagery manipulation paradigm. The reconstructed CTFs from the counter-clockwise mental rotation were inverted to reflect a clockwise response profile and these transformed CTFs were averaged with the clockwise manipulation. The delay period begins at 250ms and the imagery cue at 750ms. **A**: CTFs selectivity of evoked power across time points. **B**: CTFs selectivity of induced power across time points. **C**: Evoked CTFs profile averaged over a window during the working memory phase (160-320ms) shown in black and a average over a window corresponding to the imagery phase (750-2300ms). **D**: Induced CTFs profile averaged over a window during the working memory phase (40-700ms) shown in black and a average over a window corresponding to the imagery phase (750-2300ms). Shaded regions corresponds to a 99% confidence standard error of the mean.

During the IM phase, however, despite the fact that the CTF plots depict selectivity profiles that are less pronounced than during the WM phase, especially for the evoked activity, there is a clear shift in the selectivity of the CTFs towards the positive (clockwise) offset range. By taking an average of the CTFs from 750ms (the onset of the mental imagery phase) to 2300ms, the CTFs show a clear shift in the peak selectivity toward the orientations corresponding to a clockwise rotation of

60°, particularly for the CTF calculated from the induced activity (Figure 5C-D: blue lines).

To further examine the effect of the mental rotation of the encoded stimulus, three different average slopes of the CTFs were calculated. In the case where the mental rotation of the orientated line can be tracked down with this encoding procedure, the peak selectivity of the CTF associated with the represented orientation stimulus should not peak at the 0°, as depicted in the working memory analysis; rather, the peak selectivity should be shifted away from the center, peaking instead at the transformed orientation (+/- 60°). In order to test these changes during the imagery manipulation, two new slopes were calculated, in addition to slopes peaking 0°, in which the peak of the distribution is assumed to be 60° away from the original stimulus in both CW and CC directions. For all three orientations (-60°, 0°, +60°), average slopes were calculated over a window capturing the WM phase (200-600ms) and the IM phase (800-1800ms) (Figure 6). Note that because the CC results were inverted, all rotations should be shifted towards the positive (CW) direction. In order to determine if there is a reliable change in the slopes of the CTFs, as well as whether it is possible to track the direction in the imagery manipulation in the alpha band, two sample t-tests were conducted between the slopes corresponding to either memorized or rotated (target) orientation, and the two corresponding alternative orientations.

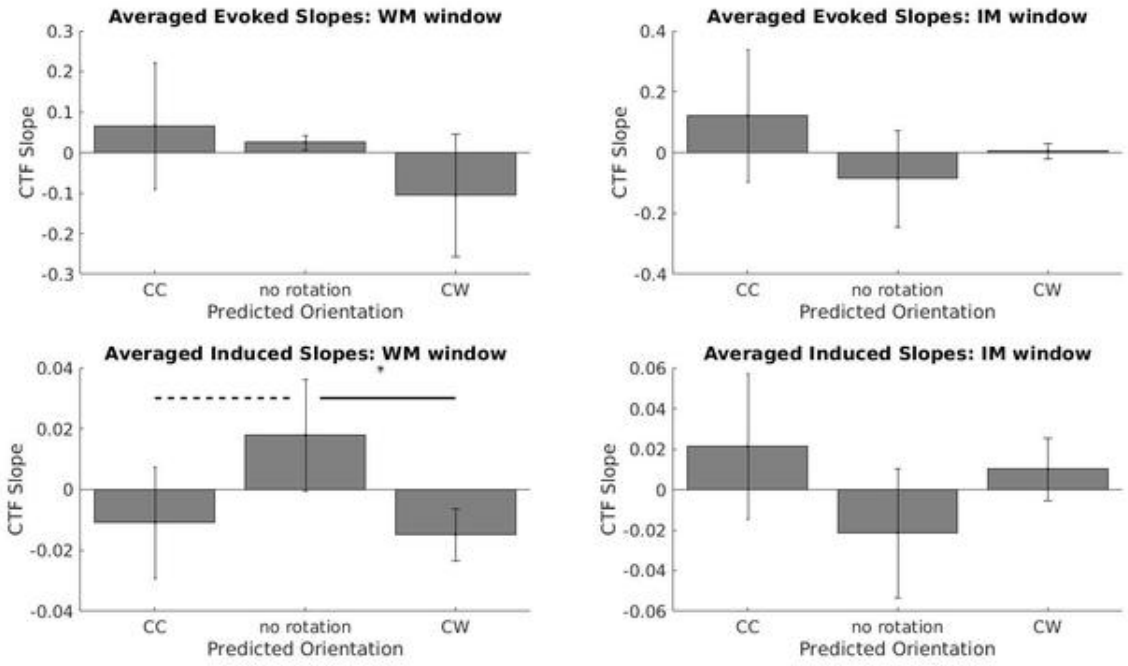

Figure 6. Average CTFs slopes comparison across evoked and induced activity, slope transformation (CW: clockwise, CC: counter-clockwise, and no transformation) as well as across working memory and imagery windows. For all trials, CW represents the target orientation of the mental rotation. Statistical comparison of induced activity between working memory showed a significant difference at $p < .005$ between CW and no rotation and only a marginal significance between CC and no rotation.

For induced activity during the WM window, the slope corresponding to the orientation of the sample WM stimulus (M= .0179,SE= .0183) was significantly more positive compared to those corresponding to orientations centered over the CW transformation (M= -.0149,SE= .0086) or CC transformation (M= -.0108,SE= .0183), t(18)= 3.01,p=.0075,d=1.42, and t(18)= 2.06,p=.055,d=.971, respectively. Thus, this confirms the previous results indicating that induced alpha activity carries information related to the specific stimuli maintained in WM. For the imagery window, however, despite the fact that the graph of the induced CTFs slopes suggests increased selectivity for CW (M= .0102,SE= .0079) and CC (M= .0102,SE= .0079) orientations and decreased selectivity for the sampled stimulus (M= -

.0213,SE= .0162) as predicted, none of these comparisons were found to be significant: CW vs. 0°, t(18)= 1.656,p= .1151,d= .781 CC vs 0°, t(18)= 1.660,p= .1142,d= .782. These same comparisons were also done with evoked CTFs slopes, which were all found non-significant: CW (M= .0659,SE= .0797) vs. sampled stimulus (M= .0252,SE= .0092) t(18)= 1.590,p= .1293,d= .06, and CC (M= -.1053,SE= .0774) and sampled stimulus t(18)= .4803,p= .6368,d= .226.

Discussion

The main objectives of this thesis were to replicate the findings of previous studies, where the patterns of activity associated with working memory representations were recreated using an encoding model, and to extend these findings by tracking the transformation of the memory representations via an imagery manipulation. By using the same paradigm as Anderson et al. (2014), the encoding model successfully identified the activity associated with the orientation of a sample stimulus during the working memory task, while providing evidence that the encoded representations actively shifted away from the original memory stimulus during the imagery period. However, while there is some evidence that the encoding model can depict that a change has occurred to the mental representation during the imagery manipulation, these findings cannot comment on the direction of the manipulation.

Precision of mental imagery

Based on the mixture-model analysis of the behavioral responses, the participants tested in this study were fairly accurate in their responses, reporting the target 95.1% of the time with an average standard deviation of only 11.13°.

Indeed, despite the fact that Foster et al. (2016) reported a very high precision (in the order of ~2°), their study only required the participants to report the feature of the stimulus (i.e. spatial location) where it was initially presented. Thus, the results here suggest that in the context of a mental rotation paradigm, participants may lose some of the fidelity of their behavioural representations due to the transformation. It is also possible that the stimuli used here were subject to an oblique effect, which is a reduced ability to accurately report an oblique line compared to a horizontal or vertical line (Furmanski & Engel, 2000). Moreover, it is difficult to determine how common this level of precision is, as although the mixture model used here is now commonly used in working memory paradigms, there have not been any previous studies utilizing this type of measure in the imagery literature. Imagery research has traditionally assessed mental rotation abilities from reaction time rather than the quality of response (Parsons, 1994; Vingerhoets, de Lange, Vandemaele, Deblaere, & Achten, 2002). Thus, while this novel approach may help answer questions about imagery performance have previously been difficult to address, it is difficult to draw definitive conclusion about the current performance of the participants on this task and their implications for mental imagery. Nonetheless, for the purpose of the current paradigm, the level of precision and proportion of guesses observed in the mental rotation task suggests that participants were able to perform the task with a high degree of accuracy.

Working memory representations

The results from the WM analysis suggest that although evoked alpha-band activity contains transient information about the memory stimulus, induced

posterior alpha-band activity can consistently and reliably encode information about the specific representations maintained in WM. Although the original Anderson et al (2014) study was retracted (see "Author-Initiated Retraction," 2015), it appears that this data produced CTF plots that are comparable to the original findings. Indeed, the original study explored a large range of frequencies (5-30Hz) and were able to demonstrate that the forward encoding model produced a reliable reconstruction of the activity associated with working memory maintenance within the induced alpha band. Thus, it seems that their conclusion that the encoding of posterior alpha activity can be used to track working memory maintenance for orientation is accurate. The results obtained in this study also support the findings from Foster et al. (2016) where they tracked spatial working memory from induced alpha activity. The current results also corroborate the role of the sensory cortex in the maintenance of visual stimulus in working memory as the literature have described, notably from fMRI MVPA studies (Harrison & Tong, 2009; Albers et al., 2013), as these effects were reported over posterior electrodes.

One interesting novel finding from the present results is that the CTFs slopes (reflecting selectivity) associated with the specific feature of the sample WM stimulus became significantly de-selected for (i.e., negative) beyond the onset of the imagery phase. This result suggests that not only did the activity accompanying the specific orientation feature initially encoded and maintained in WM disappear, but also that the CTF profile is actually differentiating the orientations that were distinct from the original sample orientation. This finding expands on a question that Anderson et al.'s (2014) addressed in their study. In one of their experiments, a cue

would appear during the retention period to inform the participant that the item held in WM was to be dropped, and the task would move on to the next trial without a probe. They observed a sharp return to baseline levels in the selectivity of the CTFs shortly after the instructions to abandon the trial were presented, compared to the normal trials that required participants to retain the object in memory until the probe. Consequently, it seems that the induced alpha band not only contains information that allows for the detection of the feature held in memory, but also that this activity is reliant on the participant's desire to hold this representation in memory. The present results extend those findings by demonstrating that the encoding model can detect whether these representations were subjected to a change or a de-selection of the sampled feature; by asking participants to rotate the object, the CTFs didn't simply become flat, reflecting a return to baseline, but instead became inverted, peaking at the orientations distinct from that of the originally encoded sample orientation. These results cannot comment on the direction of the transformation since this analysis combines the two possible rotations but does provide some evidence that changes has occurred.

Mental Imagery representations

The second objective of this study aimed to determine if it is possible to detect the changes made to a mental representation as it is subjected to a mental rotation from the same type of activity that facilitates the encoding of WM representations. Consistent with the WM analysis, the representation of the rotated stimulus is more reliable in the induced activity than in the evoked activity (Figure 4). One reason that could explain this distinction is that, despite the fact that the

onset of the imagery manipulation can be used as a time-locked event, the process of performing the alteration in the orientation feature of the stimulus is very likely to vary significantly across participants and trials. With this type of temporal variability, it would have been surprising to observe a reliable CTF selectivity in the evoked activity during the mental imagery manipulation.

However, although it appears that the CTF profiles generated from the induced alpha activity reflect the expected changes in the mental representations, and despite the fact that the original WM stimulus was negatively selected for during the IM phase of the task (Figure 3), the CTF slopes associated with the transformed (CW) as opposed to the original or alternative (CC) orientations were not significantly different during the IM phase. There are a number of possible explanations for the absence of a significant result. One possibility is that the use of a 60° rotation did not leave enough separation between the peaks of the alternative representations and their associated CTF slope calculations. Indeed, given that there are 8 orientation bins that each cover a radius of 22.5° (8 bins x 22.5° = full 180° coverage) the original orientation bin presented was only 3 bins away from the resulting orientation bin of the 60° transformation (3 x 22.5° = 67.5°), and there were only 2 bins between the clockwise and the counter-clockwise transformations. This proximity coupled with the ~10° SD of behavioural precision in the response of the participants may cause some overlap in the representational space and the associated statistical analysis, resulting in unreliable results.

It may also be the case that during the IM transformation, the neural activity produced by the internally-produced cognitive representation of the rotated

orientation contains a greater amount of noise relative to the externally-produced WM stimulus, preventing the encoding method to find reliable activity associated with the transformed feature. Since the averaged slopes for the CTFs created from the induced activity appears to depict an increased selection for the transformed feature and a negative selection for the sampled orientation, it may be possible to significantly identify the direction of transformation by increasing the sample size, and thus increasing the power of the analysis.

It is also a possibility that participants are actually representing both clockwise and counter-clockwise transformations while deciding which of the two they need to report. By adopting this kind of strategy, participants may be cycling between the two possibilities and continuously re-updating the two transformed orientations. Fiebelkorn, Saalmann, & Kastner (2013) have demonstrated that individuals, tested on a probabilistic cueing paradigm, constantly cycle their attention between the possible targets at a rhythm that corresponds to the alpha band. This location cycling may explain the intermittent presence of both rotations observed in the CTFs slopes generated from both the evoked and activity. Future studies should potentially use a modified IM task that could prevent the use of such a strategy.

Finally, it is also possible that the absence of a significant effect is evidence against the pictorial theory of mental imagery. If individuals do recreate the stimulus in their mind in a depictive manner, as Kosslyn et al. (2001) have described, then there should be enough information to encode this representation as it was done during the WM phase. On the other hand, the representational

hypothesis does not require the presence of such activity, particularly within the visual cortex, mainly because the orientation feature is held in a language-like representation. There is indication, however, that the activity detected through the encoding model suggests that at least some of the features are indeed being represented within the visual cortex, which maybe more supportive of the depictive format hypothesis.

Briefly, these findings further support the idea that induced alpha activity contains some information associated with the specific orientation of the presented stimulus to be selected by then encoding method. It is particularly the case during the replication of Anderson et al. (2014) and Foster et al. (2016), where the CTFs and their slopes strongly suggest that the orientation held in memory has fundamentally changed, but that the quality of the transformation cannot be identified.

Alpha band

Many studies have attempted to determine the role of the various types of oscillatory activity that can be detected from EEG and MEG recordings based on the paradigms and brain structures that generate this activity. Importantly, many studies have examined the oscillatory activity associated with visual working memory and found that several frequency bands are implicated in this complex process. Indeed, alpha (8-13 Hz), beta (13-30 Hz), and low-gamma (30-70 Hz) frequency bands have been observed across the fronto-parietal and visual cortices (Palva, Monto, Kulashekhar, & Palva, 2010; Sauseng et al., 2009). These frequency bands have been generally associated with the coordination of memory

conservation through constantly renewing the visual information from the visual cortex (Palva, Monto, Kulashekhar, & Palva, 2010; Jensen, Gelfand, Kounios, & Lisman, 2002). Another study has shown that theta (4-8 Hz) and gamma recordings in the posterior parietal sites were associated with maintenance but that alpha waves were a better predictor for memory capacity (Sauseng et al., 2009). These findings suggest that alpha activity does relate to processes involved in memory but may not carry any specific information. Indeed, alpha was additionally associated with distractor suppression efficiency. Sauseng et al. (2009) were able to reduce the alpha waves through rTMS, thereby creating a causal relationship between the occurrence of alpha activity and working memory functions. By disrupting alpha activity, Sauseng et al. (2009) were able to reduce working memory capacity. Their findings also suggest that alpha appears to modulate the ability to inhibit distracting information. Alpha has also been observed by many other studies to be related to visual working memory (Jensen, et al., 2002; Poliakov et al., 2014; Anderson et al., 2014) and with distractor suppression of the sensory input (Foxe & Snyder, 2011).

By comparison, there has been little investigation of a possible relationship between visual imagery and alpha oscillations. There are some studies that showed increased activity in both theta and alpha bands when participants are engaging in motor imagery (Ahn, Cho, Ahn, & Jun, 2013). Also, a greater increase in alpha activity was reported in participants who were imaging compared to hearing music (Schaefer, Vlek, & Desain, 2011).

Despite the fact that the current results do not allow for a strong conclusion that alpha-band activity supports the representation of imagined stimuli, there is

sufficient evidence that the removal of the sample WM stimulus from WM can be detected in induced alpha-band activity. One reason why alpha band activity may track with the addition and removal of a visual representation may be due to the role this oscillatory activity has with inhibitory processes. Recent studies have provided evidence in support of this interpretation of the alpha band activity (Klimesch, Sauseng, & Hanslmayr, 2007; Jensen & Mazaheri, 2010) in which the strength of alpha activity was strongly correlated with brain areas that typically engaged in tasks that were irrelevant to the particular requirements of the task. Thus, it may be the case that the information used by the encoding model that reconstructs the remembered stimulus does not pertain to the feature depicted in the sample stimulus, but rather by the inhibition of the other possible features. In other words, while alpha-band activity may be important for representing the remembered stimulus, it is through the inhibition of the non-remembered stimuli. This interpretation can very well explain why the pattern of CTFs profiles are inverted, showing strong rejection of the tuning function associated with the feature of the sampled stimulus during the imagery phase of the trial. Thus, as the remembered stimulus is removed from WM, these features become inhibited, increasing the evidence for the alternative stimuli.

Mental representations

Although the encoding method appears to reliably allow for the identification of a feature held in memory, its ability to comment on the nature (representational vs. depictive) of these cognitive representations is quite limited. Also, there is no way to determine, thus far, that participants are actually remembering the stimulus

itself. Each participant may be engaging in very different strategies to perform the task, resulting in unreliable neural signals. For instance, individuals that focus on remembering the spatial location of the intercept between the circle and the oriented line would produce activity that would very likely differ from others who are actually holding the entire stimulus in memory. However, given the fact that the encoding model is processing within-subject data, and as long as a participant is fairly consistent in their strategy, the activity associated within each variation of a particular feature should remain very similar. Indeed, regardless of the strategy used, the activity used by the encoding model still remains associated with the cognitive representation of the participant.

It also may be the case that the activity recreated by the encoding model reflects activity associated with attention or the complexity of the task at hand rather than the mental representation of the stimulus held in memory. A recent paper by Samaha, Sprague, and Postle (2016), which used a spatial attention task similar to the working memory task of Foster et al. (2016), demonstrated that the encoding model was able to reconstruct the activity associated with the location of covert attention. Indeed, many studies have provided evidence that the topography of alpha power co-varies with changes in covert attention (van Gerven & Jensen, 2009; Rihs, Michel, & Thut, 2007; Kelly, Lalor, Reilly, & Foxe, 2006). These findings may suggest that the alpha activity in this task carries information about orientation through the deployment of attention, and not by tracking an actual mental representation. This interpretation is possibly more in favour of the propositional hypothesis, as the encoding model may have used the topographical change in

covert attention in the induced alpha activity to identify the specific orientation held in memory, which could have been accomplished through processes independent of depictive representations.

On the other hand, the imagery manipulation results were not strong enough to support either pictorial or representational representation. This particular paradigm may not be able to investigate this question directly given the simplicity of the stimulus and the manipulation. Indeed, such a straightforward transformation may happen too quickly to allow the distinction between the handling of the stimulus in one's mind (suggested by the pictorial representation hypothesis) and the language-like characterization of the object (advocated by the propositional hypothesis). If the pictorial hypothesis were true, then it may have been possible to see an evolution in the selectivity of the CTFs peaking from the center at the beginning to the imagery window and move progressively towards a 60° orientation near the end of the trial. In order to observe this type of change, however, individual differences in mental rotation ability would need to be accounted for, as variation in speed will create inconsistencies in the resulting group-averaged neural signals.

Conclusions

This thesis was an attempt to replicate the findings of previous studies, which showed that working memory representations could be identified using a forward encoding model on induced EEG alpha-band activity, while also aiming to extend this technique to imagery manipulations of cognitive representations. The activity found in the induced alpha band appears to effectively allow for the

reconstruction of the remembered orientation, as has been demonstrated in the literature, and it can also demonstrate the rejection of the sampled stimulus when the representation has been modified, despite the inability to determine the direction of the change. These results support the idea that induced alpha activity contains reliable information associated with cognitive processes and can be used to identify the presence of certain features and their changes over time. Future studies and additional experiments may be required, however, to further tease apart the nature of imagery representations, and how they compare to working memory representations.

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Appendix A

Phone-Interview

"Hi, this is (insert name) calling from the (Brock Visual Cognitive Neuroscience Lab/Brock Face Perception Lab).
I'm calling you today because you've expressed interest in participating in one of our studies. Before I can schedule you for participation, I would like to tell you a bit more about the experiment, as well as ask you a few questions to make sure that you qualify.
As a participant in this study, you will be asked to respond to visual stimuli presented on a computer screen while undergoing electroencephalography (EEG). EEG is a non-invasive electrophysiological recording device that allows us to record the electrical activity from your brain indirectly via your scalp. In order to record this activity, an electrode cap will be placed on your head, and small amounts of gel placed on your head/in your hair. The cap will be held in place by an elasticized strap below your chin. Additional recording electrodes will also be placed around your eyes to measure eye-movements and eye-blinks. During the computerized tasks, you will also be asked to make judgments (i.e, button responses, mouse movements) in response to simple visual features (e.g., colours, lines) and/or faces. You may also be required to hold these visual stimuli in memory for short time periods and recall them after a short delay. Because this experiment involves differentiating colours, we will also perform a short test to assess your colour vision. Participation will take approximately 2 - 3 hours, and you will be given frequent breaks during the tasks (~ every 5 – 10 minutes). For your time we will reimburse you $15/hour ($7.50/half hour) or 1 research credit/hour (0.5 credits/half hour).
Do you have any questions about this procedure?
Would you still be interested in participating?"
If no:

"Thank you for your time. I will be sure to destroy your contact information so that we do not contact you in the future."
If Yes:
"OK, great! Before I schedule you for an appointment, I need to ask you a few questions to make sure that you qualify. These questions will assess whether you fit with in the population we are interested in for this study. Please know that these answers will be kept confidential, and if you do not qualify for the study or choose not to participate, your answers will be destroyed and no record will be kept."

QUESTIONS

1. How old are you?		
2. Do you have any condition that might affect the nervous system? (e.g. multiple sclerosis, epilepsy, fibromyalgia)	Yes	No
4. Have you ever had any serious psychiatric difficulties or mental-health issues? (e.g., Schizophrenia, clinical depression, ADHD)	Yes	No
5. Have you ever had a head injury/ concussion/ loss of consciousness? -If yes, record details.	Yes	No
6. Do you have hair extensions, braids or temporary hair dye?	Yes	No

If "yes" is answered to any of these questions:
"Thank you very much for your information. Unfortunately, based on your responses I'm afraid you do not fit within the population we are interested in studying for this particular experiment. I will be sure to delete these emails, as well as your contact information, in order to ensure that this information remains confidential. Thank you very much for your time. If you have any further questions you can feel free to contact Dr Emrich/Dr Mondloch at (provide phone number and extension)."
If "no" is answered to all of the questions:
"Thank you very much for your information. It appears based on these answers that you fit our criteria for the population we are interesting in studying for this experiment. Are you still interested in participating?"
If yes, schedule appointment.

Appendix B

INFORMED CONSENT

Date: April 15, 2014
Project title: Electrophysiological measures of selection and storage for features.

Principle Investigators (PI):
Dr. Stephen M. Emrich, Assistant Professor
Department of Psychology
(905) 688-5550 ext. 6181
semrich@brocku.ca

INVITATION
You are invited to participate in a research study being conducted in the Visual Cognitive Neuroscience Lab at Brock University. The purpose of this study is to examine the neural mechanisms involved in the perception, short-term memory and attentional selection of simple features.

WHAT'S INVOLVED
As a participant, you will be asked to respond to visual stimuli presented on a computer screen while undergoing electroencephalography (EEG). EEG is a non-invasive electrophysiological recording device that allows us to record the electrical activity from your brain indirectly via your scalp. In order to record this activity, an electrode cap will be placed on your head, and small amounts of gel placed on your head/in your hair. The cap will be held in place by an elasticized strap below your chin. Additional recording electrodes will also be placed around your eyes to measure eye-movements and eye-blinks. During the computerized tasks, you will also be asked to make judgments (i.e, button responses, mouse movements) in response to simple visual features (e.g., colours, lines) and/or faces. You may also be required to hold these visual stimuli in memory for short time periods and recall them after a short delay. Because this experiment involves differentiating colours, we will also perform a short test to assess your colour vision. Participation will take approximately 2 - 3 hours, and you will be given frequent breaks during the tasks (~ ever 5 – 10 minutes).

POTENTIAL RISKS AND BENEFITS
Participation in this research will help advance our understanding of how the human brain processes visual information. In addition, for your time you can either receive (a) credit (0.5 credit hours/30 minutes) for experiment participation as part of a requirement for courses at Brock University, such as PSYC 1F90 (where applicable), **OR** (b) a remuneration of $15/hour (i.e., $7.50 for every 30 minutes). There are no known or anticipated risks associated with participation in this study.

CONFIDENTIALITY
All of the information provided in this study will be identified by an arbitrary participant number and will not be linked to your identity, in any way.
Data collected during this study will be stored in the laboratory of Dr. Stephen Emrich or Dr. Cathy Mondloch. Only researchers in these laboratories will have access to these materials. Data will be kept for 10 years following publication, after which time the electronic files will be erased and paper copies will be shredded.

VOLUNTARY PARTICIPATION
Participation in this study is voluntary. If you wish, you may decline to answer any questions or participate in any component of the study. Further, you may decide to withdraw from this study at any time and may do so without any penalty or loss of benefits to which you are entitled. If you decide to withdraw from the study after beginning the computerized portion of the experiment, your data will be destroyed immediately. If you choose to withdraw after completion of the study you data cannot be destroyed because it will be identified with an anonymous participant number.

PUBLICATION OF RESULTS
Results of this study may be published in professional journals and presented at conferences. Feedback about this study will be available once the study is complete by contacting Dr. Stephen Emrich at the address or phone number listed at the top of this consent form. Only information about the results of the entire study will be available, not information on individual performance.

CONTACT INFORMATION AND ETHICS CLEARANCE
If you have any questions about this study or require further information, please contact Stephen Emrich or Cathy Mondloch using the contact information provided above. This study has been reviewed and received ethics clearance through the Research Ethics Board at Brock University (File # **[13-272]**). If you have any comments or concerns about your rights as a research participant, please contact the Research Ethics Office at (905) 688-5550 ext. 3035 or reb@brocku.ca

Thank you for your assistance in this project. Please keep a copy of this form for your records.

CONSENT FORM
I agree to participate in this study described above. I have made this decision based on the information I have read in the Information-Consent Letter. I have had the opportunity to receive any additional details I wanted about the study and understand that I may ask questions in the future. I understand that I may withdraw this consent at any time.

Name: _____

Signature: _____ Date: _____

Witnessed by:

Name: _____

Signature: _____ Date: _____

FEEDBACK
I would like to receive the summary of the research results. (check one):

YES_____

NO _____

email address to send research summary to: _____

For participation in this experiment, I wish to receive: **Experiment Credit _____**
(check one) **Paid remuneration _____**

Hours Participated: _____ Credits/Reimbursement Received:_____

Course to receive credit: _____

Experimenter Signature: _____ Date:_____